



Contrasting responses to long-term climate change of carbon flows to benthic consumers in two different sized lakes in the Baltic area.

Simon Belle ^{a, b, *}, Rene Freiberg ^b, Anneli Poska ^c, Helen Agasild ^b, Tiiu Alliksaar ^c, Ilmar Tõnno ^b

^a Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

^b Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartumaa, Estonia

^c Institute of Geology, Tallinn University of Technology, Tallinn, Estonia

ARTICLE INFO

Article history:

Received 23 November 2017

Received in revised form

16 March 2018

Accepted 16 March 2018

Available online 30 March 2018

Keywords:

Climate change

Benthic food web

Large lake

Carbon stable isotope

Subfossil chironomid

ABSTRACT

The study of lake sediments and archived biological remains is a promising approach to better understand the impacts of climate change on aquatic ecosystems. Small lakes have been shown to be strongly sensitive to past climate change, but similar information is lacking for large lakes. By identifying responses to climate change of carbon flows through benthic food web in two different sized lakes, we aimed to understand how lake morphometry can mediate the effects of climate change. We reconstructed the dynamics of phytoplankton community composition and carbon resources sustaining chironomid biomass during the Holocene from the combined analysis of sedimentary pigment quantification and carbon stable isotopic composition of subfossil chironomid head capsules ($\delta^{13}\text{C}_{\text{HC}}$) in a large lake in the Baltic area (Estonia). Our results showed that chironomid biomass in the large lake was mainly sustained by phytoplankton, with no significant relationship between $\delta^{13}\text{C}_{\text{HC}}$ values and temperature fluctuations. We suggest that lake morphometry (including distance of the sampling zone to the shoreline, and lake volume for primary producers) mediates the effects of climate change, making large lakes less sensitive to climate change. Complementary studies are needed to better understand differences in organic matter dynamics in different sized lakes and to characterize the response of the aquatic carbon cycle to past climate change.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

Identification of energy pathways through food webs is essential to understand the ecosystem functioning (Lindeman, 1942) and can be used to assess impacts of climate change, one of the most important ongoing threats to inland aquatic ecosystems (Goldman et al., 2012). Mechanisms by which climate change affects lake ecosystems can be summarized by the conceptual Energy-mass framework (Leavitt et al., 2009). According to this framework, the broader catchment area and the lake itself can act as environmental filters that mediate climate change effects (Blenckner, 2005). The impacts of climate change on lake carbon cycling are still poorly understood and similar climate signals can induce contrasting lake responses that depend on the catchment properties. For example in

response to global warming, the Arctic landscape (i.e., tundra) became greener leading to dramatic decreases in phosphorus concentrations in high Arctic lakes (Huser et al., 2018), whereas glacier retreats in the Nepalese Himalayan watershed induced increase in solute concentrations in nearby lakes (Salerno et al., 2016).

Due to the key role of sediments in recycling organic matter (OM) in lakes (Meyers and Ishiwatari, 1993), carbon flows to benthic consumers can represent an integrative proxy to understand the functioning of the entire aquatic food webs (Vadeboncoeur et al., 2002). Benthic food webs can be sustained by organic carbon from terrestrial sources (allochthonous) and autochthonous carbon from aquatic primary producers (Jones et al., 1998; Lau et al., 2014). The availabilities from these two sources in the environment can be highly variable in both space and time (Sylväranta et al., 2006; Belle et al., 2015a; Berggren et al., 2015). Moreover, complex transfer pathways (direct consumption and/or bacterial pathways; Cole et al., 2006; Jansson et al., 2007) make

* Corresponding author. Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden.

E-mail address: simon.belle@slu.se (S. Belle).

tracking carbon flows to aquatic consumers difficult. While allochthonous organic carbon is often not preferentially assimilated by aquatic consumers due to its lower nutritive quality than in-lake primary production (Guo et al., 2016; Crenier et al., 2017), allochthonous carbon can become an important resource to aquatic consumers under specific conditions (Carpenter et al., 2005). Indeed, important contributions of allochthonous OM to the diet of aquatic consumers were found for small and low-production lakes (Wilkinson et al., 2013), with strong connectivity between terrestrial and aquatic systems. The lowest allochthonous contribution to aquatic consumers was found during periods of high in-lake primary production (Rautio et al., 2011; Berggren et al., 2015). Allochthonous contributions to aquatic consumers thus are negatively correlated with aquatic primary productivity and lake size due to the increasing availability of autochthonous resources and limited connectivity between terrestrial and aquatic systems (Tanentzap et al., 2017). Therefore, carbon flows through benthic food webs of different sized lakes could exhibit different responses to past climate change.

Analysis of biological remains archived in lake sediments is a powerful approach to reconstruct the past dynamics of aquatic food webs (Walker, 2001), and to understand the effect of past climate change on aquatic food webs. The Chironomidae (Arthropoda; Diptera; Nematocera) are non-biting midges whose larvae can live in superficial lake sediments and are often a dominant group in benthic secondary production of lakes. They are considered a keystone taxonomic group because they are involved in the recycling of OM in sediments (Nogaro et al., 2009) and form an important trophic link between aquatic primary producers and top predators in lakes (i.e., benthic/pelagic coupling; Goedkoop and Johnson, 1996). The most sclerotized part of their exoskeleton, the head capsule (HC), is morphologically and chemically well-preserved in sediments after each moulting (Verbruggen et al., 2009). Stankiewicz et al. (1997) reported that chitin, the most important compound of chironomid exoskeleton, can be chemically preserved for up to 25 million years. The difference between the carbon stable isotopic composition (expressed as $\delta^{13}\text{C}$) of a food and its consumer, the trophic fractionation, is considered to be very low or negligible for chironomid larvae (Goedkoop et al., 2006). Moreover, the offset between larvae and their HC is assumed to be constant (Frossard et al., 2013a). Differences in fractionation by primary producers (allochthonous vs. autochthonous producers; Jones et al., 1998; Vuorio et al., 2006) and bacteria (e.g., methanogenesis and methanotrophy; Whiticar, 1999) can lead to food resources at the base of aquatic food webs that differ in their $\delta^{13}\text{C}$ values. Nevertheless, many biological and biochemical processes sometimes lead to overlaps in autochthonous and allochthonous isotopic baselines (Smyntek et al., 2012). The use of complementary proxies, such as sedimentary pigments, provides additional insights into changes in organic carbon dynamics in lake sediments (Guilizzoni et al., 2011).

$\delta^{13}\text{C}$ analysis of chironomid remains ($\delta^{13}\text{C}_{\text{HC}}$) has been used to provide long-term reconstruction of changes in carbon resources sustaining chironomid biomass (Wooller et al., 2012; van Hardenbroek et al., 2014). Chironomid $\delta^{13}\text{C}$ -based reconstructions focused on the effects of climate change have mainly been conducted on small lakes. Those studies showed that chironomid biomass was sustained by a combination of allochthonous, autochthonous, and CH_4 -derived OM, with relative contributions correlated with temperature fluctuations (Wooller et al., 2012; van Hardenbroek et al., 2013; Belle et al., 2017b, Belle et al., 2018). Chironomid biomass was sustained mainly by aquatic OM except under two specific climate and environmental conditions. Specifically, relatively high terrestrial contributions to chironomid biomass occurred during cold and low in-lake production periods,

whereas important incorporation of CH_4 -derived carbon to benthic consumers was found during anoxic events that co-occurred with warm periods. Nevertheless, very little is known about climate-induced changes in the carbon resources that sustain benthic consumers in large lakes and complementary studies following a similar approach are still needed.

The goal of this study was to test how lake morphometry can act as an environmental filter that mediates the effects of climate change on carbon flows through benthic food webs. Long sediment cores were collected in the deepest part of a large lake in north-eastern Europe (Lake Peipsi, Estonia) and temporal changes in carbon resources sustaining chironomid biomass were assessed using carbon stable isotope analysis of subfossil chironomid HC. These results were compared to those from Lake Tollari, a small boreal lake nearby, previously published by Belle et al. (2017b). We hypothesized that changes in food sources at the base of the benthic food web of the large lake would rely more strongly on pelagic processes due to the higher availability of aquatic primary production and a limited connectivity with terrestrial environment.

2. Material and methods

2.1. Study site

Lake Peipsi is the fourth largest lake in Europe with an area of 3555 km² and a very large catchment area (Fig. 1A; Table 1). The maximal water depth of the main lake basin (Lake Peipsi proper) reaches 12.9 m (Fig. 1C). The landscape transformation throughout Estonia due to agricultural practices began during the Iron Age (from ca. 2.5 kyr cal. BP; Poska et al., 2004), but its impact on Lake Peipsi remained very low or negligible (Leeben et al., 2010; Kisand et al., 2017). The industrialisation and urbanisation accompanied by massive use of mineral fertilizers and ineffective waste water treatment caused eutrophication to accelerate dramatically during the 20th century (Leeben et al., 2008). The sediment core was retrieved from the deepest part of the lake using a Russian-type peat corer, with the coring location approximately 15 km from the nearest shoreline (Fig. 1C and 1D). Details on the coring and dating methods are in Leeben et al. (2010). The number, name, and non-calibrated age of each radiocarbon date are given in Appendix 1. All sample depths were converted to calibrated year BP (IntCal13; Reimer et al., 2013; kyr cal. BP, with 0 cal. BP = AD 1950) according to the age-depth model (Fig. 1D). Average sedimentation rates were estimated to be about 0.3 mm yr⁻¹ for Lake Peipsi. To avoid any potential degradation, sediment samples were stored in a freezer at -20 °C.

Temperature variability during the Holocene has been well studied in the Baltic area (e.g., Seppä and Poska, 2004; Holmström et al., 2015) and all reconstructions have provided similar and characteristic temporal trends. We assumed that climate variability in the two studied lakes was similar, and used a reconstruction of the mean air temperature of the warm months (May, June, July, and August; T_{Summer} ; °C) obtained from transfer functions of pollen and spore analysis results from the Lake Tollari record Belle et al. (2017b).

2.2. Sedimentological and chironomid remains analyses

To assess the overall OM input, sediment cores were sliced into continuous 1-cm thick layers and OM content analysed according to the loss-on-ignition method. Results were then expressed in terms of percentage of dry weight (% of dry weight). We also analysed photosynthetic pigments archived in sediments to track temporal changes in the trophic state of Lake Peipsi and past phytoplankton community composition dynamics. Sedimentary

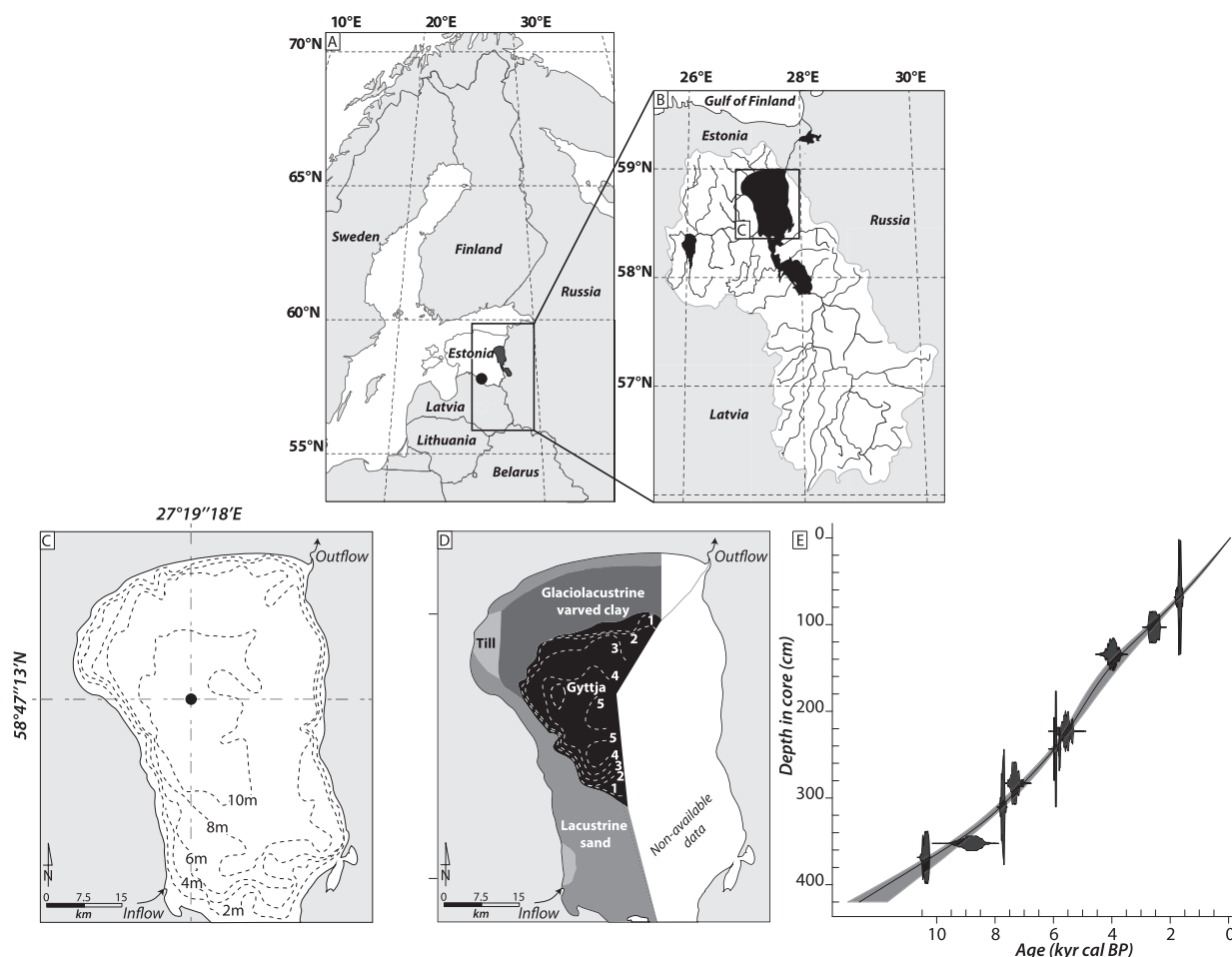


Fig. 1. (A) Geographical location of Lake Tollari (57°45'6"N, 26°20'32"E, black dot), and Lake Peipsi (58°47'13"N, 27°19'18"E, coordinates of the coring position) with its catchment area (B). (C) Bathymetric map of Lake Peipsi. Black dot indicates the coring position. (D) Map of the bottom deposits of Lake Peipsi, modified after Hang et al., (2001). Numbers and isolines show the gyttja deposit thickness (up to 5 m). Age-depth model built by smooth-spline interpolations of the core collected in Lake Peipsi (E). Details concerning the calibration of radiocarbon dates are in Appendix 1. All sample depths were then converted to calibrated year BP (kyr cal. BP, with 0 cal. BP = AD 1950) according to the age-depth model. The age-scale of Lake Peipsi sediment core ended at 10.4 kyr cal. BP (see details in Leeben et al., 2010).

Table 1
Morphological characteristics of Lake Peipsi and Lake Tollari. "A_CA_L" refers to the ratio between catchment and lake areas.

Parameters	Lake Peipsi	Lake Tollari
Elevation (m a.s.l.)	30	97.5
Max. water depth (m)	12.9	9.9
Lake area (km ²)	3555	0.057
Catchment area (km ²)	47800	0.377
A _C A _L	13.4	6.6
Volume (km ³)	25	—

pigment samples were collected every 2 cm ($n = 183$) and analysed following recommendations by Leavitt and Hodgson (2002). Briefly, sedimentary pigments were extracted from freeze-dried samples using a solution of acetone and methanol (80:20 v:v at -20°C in the dark) for 24 h. Pigment extracts then were filtered through a $0.45\ \mu\text{m}$ filter. Reversed-phase high-performance liquid chromatography (RP-HPLC), with a Shimadzu Prominence (Japan) series binary gradient system with a photodiode array (PDA) and fluorescence detectors was used to separate sedimentary pigments (see Tamm et al., 2015 for more details). Peaks were identified and quantified from commercially available external standards (DHI; Denmark). β -Carotene (β -car) was then selected to indicate the

total algal abundance and primary production, while Fucoxanthin (Fuco) and Echinonone (Echin) were selected to indicate abundances of diatoms and cyanobacteria, respectively (Waters et al., 2013; Deshpande et al., 2014). Results were expressed as nanomoles per gram of OM (nmol g OM^{-1}).

1-cm tick sediment samples were collected at 2 or 3 cm intervals along the Lake Peipsi core ($n = 110$) and used for stable isotopic analyses. Approximately 500 mg of wet sediment was dried at 60°C for 72 h and ground to a fine powder for each sample. Subsequently, carbonates were removed using small additions ($50\ \mu\text{L}$) of HCl (3.7%) in silver capsules. After further drying at 60°C for 72 h, ca. 3 mg of carbonate-free sediment was loaded into a tin capsule for stable isotope analysis. Carbon stable isotopic compositions of sedimentary OM ($\delta^{13}\text{C}_{\text{OM}}$) were analysed using an isotope ratio mass spectrometer interfaced with an elemental analyser (EA-IRMS) at INRA Nancy (Champenoux). Results were expressed as the delta notation with Vienna Pee Dee Belemnite as the standard: $\delta^{13}\text{C}(\text{‰}) = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$; where $R = {}^{13}\text{C}/{}^{12}\text{C}$. Replication of internal standards (with a target weight of 3 mg) yielded an analytical error (1σ) of 0.02‰ ($n = 15$). Then, the rest of each sediment sample was used for chironomid analysis. Sediment samples were pre-treated using successive washings with NaOH (10%) and HCl (10%) solutions and sieved through a $100\ \mu\text{m}$ mesh according to recommendations by Schimmelmann and DeNiro

(1986) and van Hardenbroek et al. (2009). Carbon stable isotope composition of chironomid remains ($\delta^{13}\text{C}_{\text{HC}}$) belonging to the morphotype *Chironomus plumosus*-type (based on the classification by Brooks et al., 2007) was analysed using an EA-IRMS at INRA Nancy (Champenoux). To avoid misleading interpretations due to incomplete carbon turn-over during larval development, only HCs belonging to the 4th larval instar were selected individually (Frossard et al., 2013a). Results were expressed according to the delta notation (see above). Replication of sample measurements from internal laboratory standards (with a target weight of 20 μg) produced analytical errors (1σ) of $\pm 0.2\text{‰}$ ($n = 23$). 15 to 20 HC were loaded into tin capsules to reach sample weight of at least 20 μg . When too few HC occurred in a single sediment sample, a few consecutive samples were pooled together. The new sample ages of the pooled sediment layers were averaged to give a new sample age. A total of 76 chironomid samples were analysed.

2.3. The Lake Tollari dataset

Lake Tollari (57°45'6"N, 26°20'32"E; 97 m a.s.l.) is a small lake (5.7 ha; Table 1) located in the Karula upland, Estonia (Fig. 1A). The sediment core was retrieved from the deepest part of the lake at ca. 150 m of the nearest shoreline; details concerning coring and dating methods were previously reported by Belle et al. (2017b). The Lake Tollari record was studied using same methods with the exception of morphotype (Belle et al., 2017b), carbon stable isotopic analyses were performed on *Chironomus anthracinus*-type morphotype HC. Intensive human activities in the catchment of Lake Tollari were recorded during the last ca. 1.5 millennia, which corresponded approximately to the uppermost 2.5 m of sediment. Increasing agriculture led to dramatic decreases in forest cover and widespread crop cultivation that impacted the lake carbon cycling (Belle et al., 2017b). The comparison of two different-sized lakes in the same climate zone is a first step to test the hypothesis of contrasting responses to past climate change of carbon flows to benthic consumers due to the differences in lake morphometry and terrestrial connectivity.

2.4. Statistical analysis

To visually track the principal temporal trend in Lake Peipsi data, time series were analysed using additive models (GAM; fitted using the *mgcv* package for R; Wood, 2011). Temperature, content, composition of the sedimentary OM, and lake trophic status were expected to have a significant and potentially non-linear influence on carbon resources fuelling benthic consumers. Thus, statistical relationships between Lake Peipsi $\delta^{13}\text{C}_{\text{HC}}$ values and explanatory variables (T_{summer} , OM content, $\delta^{13}\text{C}_{\text{OM}}$, and β -car) were examined using a GAM approach, with a continuous-time first-order autoregressive process to account for potential temporal autocorrelation (Simpson and Anderson, 2009).

To compare temporal changes in carbon sources sustaining chironomid biomass in lakes Peipsi and Tollari, we modelled the $\delta^{13}\text{C}_{\text{HC}}$ time series using a GAM approach following recommendations by Simpson and Anderson (2009) assuming that temporal dynamics followed a non-linear trend over time. Significance of the fitted trends was checked using standard statistical inference for GAMs (Wood, 2011). Moreover, patterns in temporal trends were evaluated using the first derivative of the fitted GAM and associated 95% confidence interval estimated using the finite difference method (using the *tsgam* package for R; available online from <https://github.com/gavinsimpson/tsgam>), following the procedure of Bennion et al. (2015). Negative first derivatives corresponded to a decreasing trend in $\delta^{13}\text{C}_{\text{HC}}$ data whereas positive first derivatives corresponded to an increasing trend. All statistical tests and

graphical displays were performed using R 3.4.0 statistical software (R Core Team, 2017).

3. Results

OM contents in Lake Peipsi sediment records ranged from 3.9 to 28.9% (Fig. 2). The temporal trend of OM rose gradually during the first part of the Holocene and remained nearly constant during the second part of the record (Fig. 2). The $\delta^{13}\text{C}_{\text{OM}}$ values ranged from -32.4 to -29.8‰ (Fig. 2), but the $\delta^{13}\text{C}_{\text{OM}}$ trend gradually increased until the present day. All sedimentary pigment concentrations (β -car, Echin and Fuco) increased from 10.5 to ca. 8 kyr cal. BP (Fig. 2). β -car and Echin reached maximum values during the Holocene Thermal Maximum (Fig. 2). Then, Echin concentrations gradually decreased to intermediate values after ca. 4.5 kyr cal. BP, β -car concentrations remained nearly constant, whereas Fuco continued to increase during the second part of the Holocene (Fig. 2). Subfossil chironomid $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{HC}}$) ranged from -36.9 to -27.1‰ , with average values of -31‰ (Fig. 2). Despite the range of the explanatory variables (Fig. 2), the relationships were only significant between $\delta^{13}\text{C}_{\text{HC}}$ and T_{summer} , and between $\delta^{13}\text{C}_{\text{HC}}$ and $\delta^{13}\text{C}_{\text{OM}}$ (Fig. 3; Table 2), but none of these models explained more than a small percentage of the variance in $\delta^{13}\text{C}_{\text{HC}}$ (Table 2).

GAMs fitted to the $\delta^{13}\text{C}_{\text{HC}}$ time series of Lake Peipsi (this study) and Lake Tollari (Belle et al., 2017b) are summarized in Table 3. GAMs showed strong nonlinear relationships for both lakes ($F = 6.91$, p -value < 0.001 , $\text{edf} = 5.86$; and $F = 9$, p -value < 0.001 , $\text{edf} = 2.99$ for Lake Tollari and Lake Peipsi, respectively) revealing significant temporal trends, however the coefficient of determination was lower for Lake Peipsi ($R^2 = 0.23$; Table 3). First derivatives of GAMs for Lake Tollari were only significantly different from 0 from ca. 10.5 to 8.5 kyr cal. BP with negative values (Fig. 4). Then, the first derivative switched to positive from 8 to 4.5 kyr cal. BP (Fig. 4), but this increase was not statistically significant and the confidence interval intercepted 0 until ca. 1.5 kyr cal. BP (Fig. 4). First derivatives of GAMs fitted to Lake Peipsi data did not reveal any significant pattern (Fig. 4), confirming the absence of trend in Lake Peipsi $\delta^{13}\text{C}_{\text{HC}}$ values (Fig. 2).

4. Discussion

4.1. Lake ontogeny and temporal changes in the origin of organic matter in lake sediments

Organic carbon dynamics in lake sediments was first quantitatively reconstructed using loss-on-ignition analysis. For Lake Peipsi, OM content in sediments was very low during the first stage of the Early Holocene (Fig. 2). Then, the OM content gradually increased due to increasing water level and a warmer climate (Hang et al., 2008) and then remained almost constant until modern days (Fig. 2). Indeed, rapid warming observed during the first millennia of the Holocene (i.e., Early Holocene, from 10.5 to ca. 8 kyr cal. BP), probably enhanced the effect of natural eutrophication (Anderson et al., 2008) and caused the observed increase in OM contents (Fig. 2). Similar trends in OM accumulation have frequently been found in Holocene sediment records from temperate lakes (e.g., Magny et al., 2012), boreal lakes (e.g., Punning et al., 2005) and Arctic lakes (e.g., Anderson et al., 2009).

Organic carbon dynamics in lake sediments also were qualitatively reconstructed using combined analyses of sedimentary pigments and carbon stable isotopic compositions of sedimentary OM ($\delta^{13}\text{C}_{\text{OM}}$). Rapid increase in photosynthetic pigment concentrations during the Early Holocene revealed major changes in the lake trophic status (Fig. 2), as reported in previous studies (Digerfeldt and

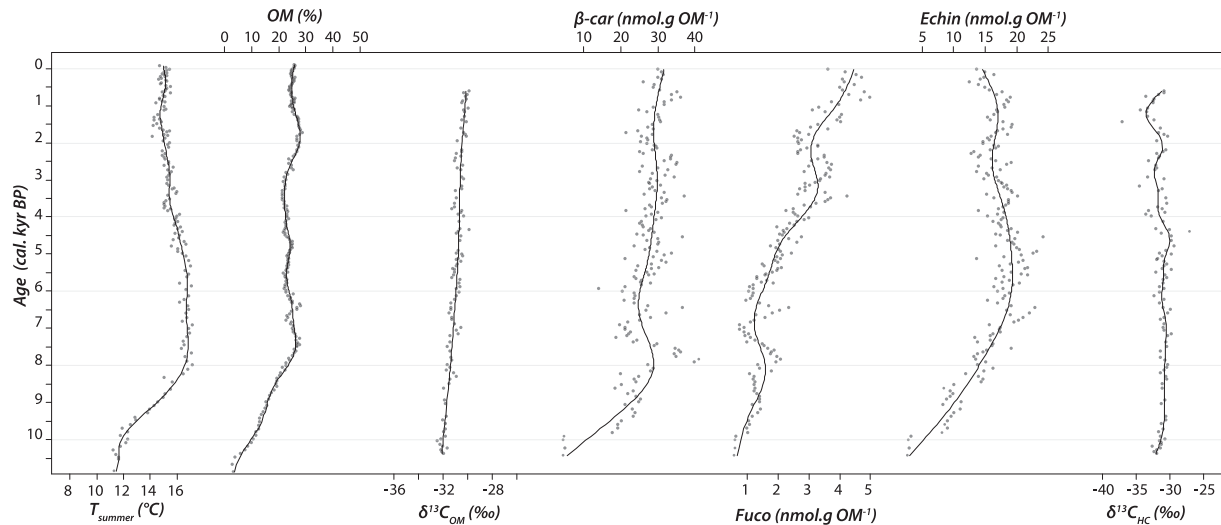


Fig. 2. The stratigraphic diagram shows the pollen-based mean summer temperature reconstruction (T_{summer} ; °C, Belle et al., 2017b), Lake Peipsi organic matter content (OM; %), carbon stable isotopic composition of sedimentary organic matter ($\delta^{13}\text{C}_{\text{OM}}$; ‰), the temporal trend in sedimentary pigments (β -car, Fuco, Echin, expressed in nmol g OM⁻¹), and carbon stable isotopic composition of chironomid remains ($\delta^{13}\text{C}_{\text{HC}}$; ‰).

Lake Peipsi

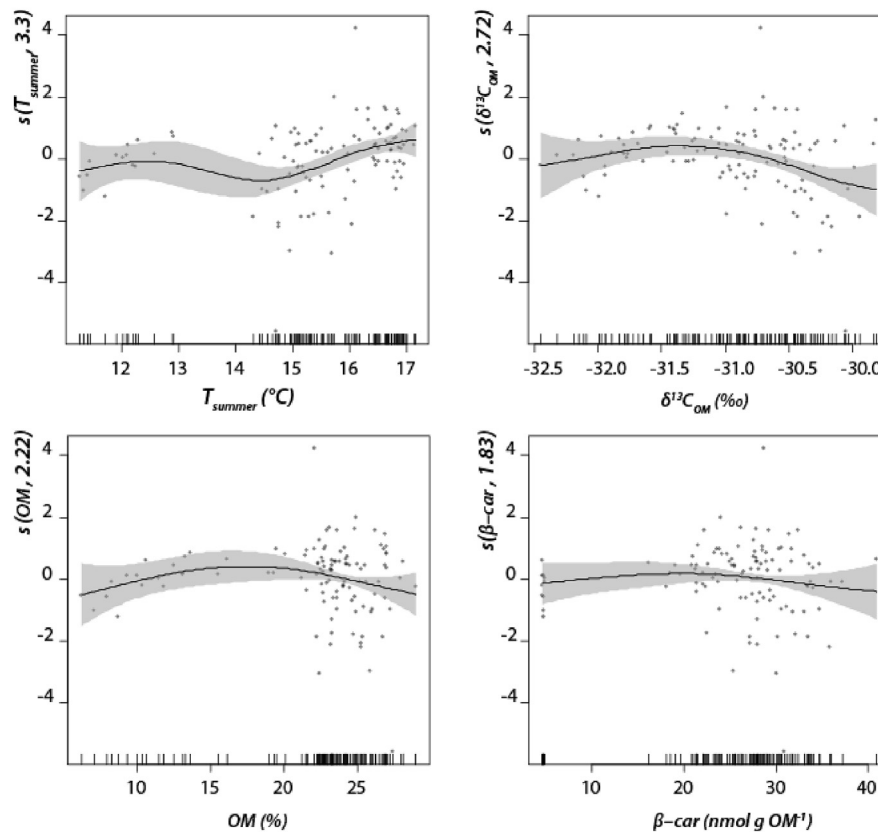


Fig. 3. Fitted smooth function between explanatory variables (T_{summer} ; $\delta^{13}\text{C}_{\text{OM}}$; OM; and β -car) and $\delta^{13}\text{C}_{\text{HC}}$ values from generalized additive models (GAM). Grey surface marks the 95% confidence interval of the fitted function. On the x-axis, black ticks show the distribution of observed values for variables. Numbers in brackets on the y-axis are the effective degrees of freedom (edf) of the smooth function.

Håkansson 1993; Reuss et al., 2010). The highest values of aquatic primary production occurred during the Holocene Thermal Maximum (Fig. 2), whereas the Fuco marker pigment continued to increase until present days. Although aquatic primary production

dramatically increased during the Early Holocene according to sedimentary pigment interpretations (Fig. 2), we found very small temporal changes in $\delta^{13}\text{C}_{\text{OM}}$ values. In contrast, the study of OM dynamics in small Lake Tollari in the same area (Belle et al., 2017b)

Table 2

Summary of statistics for the generalized additive models (GAM) fitted with a Gaussian distribution to the carbon stable isotopic composition of chironomid remains ($\delta^{13}\text{C}_{\text{HC}}$; ‰) in Lake Peipsi sediments. The explanatory variables were: pollen-based mean summer temperature reconstruction (T_{summer} ; °C), organic matter content (OM; %), carbon stable isotopic composition of sedimentary organic matter ($\delta^{13}\text{C}_{\text{OM}}$; ‰), and β -Carotene (β -car; nmol g OM⁻¹). “*edf*” refers to the effective degrees of freedom.

Lake Peipsi	R ²	Intercept	p	edf	F	p
$\delta^{13}\text{C}_{\text{HC}} \sim s(T_{\text{summer}})$	0.17	−31.3	<0.001	3.3	4.69	<0.001
$\delta^{13}\text{C}_{\text{HC}} \sim s(\delta^{13}\text{C}_{\text{OM}})$	0.13	−31.3	<0.001	2.72	3.91	<0.05
$\delta^{13}\text{C}_{\text{HC}} \sim s(\text{OM})$	0.05	−31.3	<0.001	2.22	1.84	0.18
$\delta^{13}\text{C}_{\text{HC}} \sim s(\beta\text{-car})$	0.02	−31.3	<0.001	1.83	0.85	0.4

Table 3

Summary of statistics for the generalized additive models (GAM) fitted with a Gaussian distribution to the time-series of $\delta^{13}\text{C}_{\text{HC}}$ values (‰) of chironomid remains in Estonian lake sediments. “*edf*” refers to the effective degrees of freedom. Fitted trend splines from GAM were then used to estimate the first derivative.

Lake Tollari	Intercept	t-value	p
$\delta^{13}\text{C}_{\text{HC}} \sim s(\text{Age})$	−34.6	−132.8	<0.001
R ² = 0.55		F	p
Terms	edf		
s(Age)	5.86	6.91	<0.001
Lake Peipsi	Intercept	t-value	p
$\delta^{13}\text{C}_{\text{HC}} \sim s(\text{Age})$	−31.3	−315	<0.001
R ² = 0.23		F	p
Terms	edf		
s(Age)	2.99	9	<0.001

revealed a temporal trend in $\delta^{13}\text{C}_{\text{OM}}$ values that reflected changing contributions of allochthonous and aquatic OM to lake sediments. For Lake Peipsi, average $\delta^{13}\text{C}_{\text{OM}}$ values indicated the dominance of aquatic OM in lake sediments (around −32‰, Fig. 2; Vuorio et al., 2006). The observed trend suggests that the proportion of allochthonous OM in lake sediments did not have a significant influence on the carbon stable isotope composition of sedimentary OM. The slight, gradual increase observed in $\delta^{13}\text{C}_{\text{OM}}$ values may reflect a long-term decrease in concentrations and/or an increase in the carbon stable isotopic composition of the dissolved inorganic carbon taken up by aquatic primary producers (Catalan et al., 2009; Smyntek et al., 2012) leading to progressive changes in phytoplankton $\delta^{13}\text{C}$ values.

The distance to the shoreline and/or to inflow of large rivers could change the allochthonous carbon availability at the sampling location and/or change its nutritive value (Tanentzap et al., 2017). Indeed, the long-distance transport from the terrestrial environment to the profundal and central zones of Lake Peipsi may cause physical, photo-chemical, and biological degradation leading to low availability and nutritive value of allochthonous OM in the deepest zone of Lake Peipsi. The coring site was currently ca. 15 km from the nearest shoreline (Fig. 1C and 1D), and was also far from the shoreline during lowest water level observed during Early Holocene (corresponding approximately to the gyttja deposit, Fig. 1D, Hang et al., 2008). Moreover, Lake Peipsi has a large water volume leading to a very low sediment surface to epilimnion volume ratio (Table 1). Thus, large amounts of aquatic OM may be produced in Lake Peipsi, which becomes available to support benthic consumers after deposition. Reconstructions of sedimentary carbon dynamics of large lakes based on bathymetric and spatial approaches should further be developed to better understand the influence of lake morphometry such as distance to the shoreline and major inflows on lake carbon cycling and aquatic food webs. The combination of sedimentary pigments and compound-specific stable isotope analyses (Hockun et al., 2016) could also provide complementary

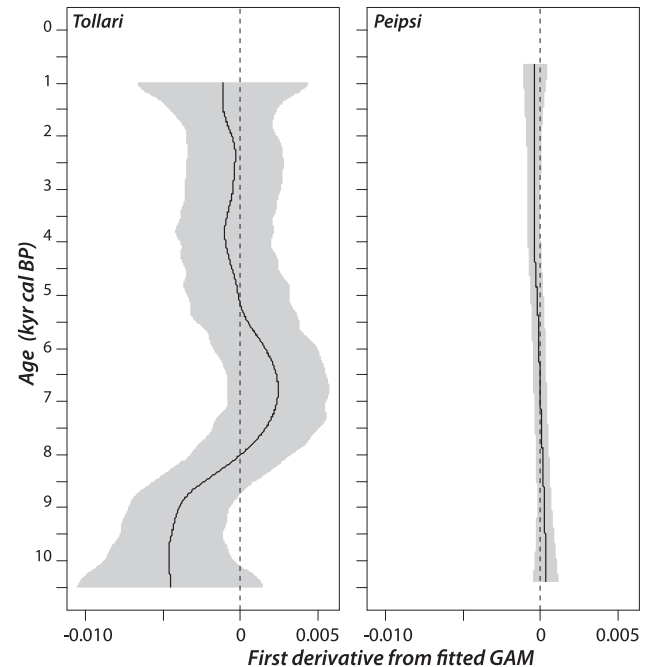


Fig. 4. Temporal dynamics of the first derivative of generalized additive models (GAM) fitted to $\delta^{13}\text{C}_{\text{HC}}$ data from Estonian lake sediments. Negative values indicate a decreasing trend in $\delta^{13}\text{C}_{\text{HC}}$ data. Grey surface marks the 95% confidence interval.

insights about pathways of sedimentary OM in lake sediment records.

4.2. Effects of lake morphometry on the response of benthic food web to climate change

Small lakes have been shown to be strongly sensitive to past climate change (Wooller et al., 2012; van Hardenbroek et al., 2013; Rantala et al., 2015; Belle et al., 2017a, Belle et al., 2018), but very little is known about large lakes. In Estonia, reconstruction of the Holocene carbon flows through benthic food web in a small lake revealed complex changes in carbon sources (i.e., from terrestrial and aquatic origins) and energy pathways (i.e., benthic and pelagic processes), and a strong relationship with temperature fluctuations (Belle et al., 2017b). Due its high nutritive value (Guo et al., 2016), aquatic consumers were more strongly reliant on phytoplankton. By contrast, allochthonous OM was an important resource sustaining chironomid biomass during the coldest and least productive Holocene period, providing consistent results from small and oligotrophic lakes (Goedkoop and Johnson, 1992). Similar investigations conducted in Lake Peipsi (a large boreal lake) did not reveal the same relationship with temperature fluctuations (Figs. 2 and 4). Despite the large gradient covered by climate conditions (Ilvonen et al., 2016), OM content (Leeben et al., 2008), lake trophic status (Fig. 2), and water-level fluctuations (Hang et al., 2008), the $\delta^{13}\text{C}_{\text{HC}}$ values remained nearly constant over time (Fig. 2). According to average $\delta^{13}\text{C}_{\text{HC}}$ values (Fig. 2), chironomid biomass may be mainly sustained by aquatic OM. This phenomenon could be due to the OM dynamics in Lake Peipsi sediment. Owing to potential effects of distance of the shoreline, and large lake volume, aquatic primary producers may be highly available for benthic consumers even during periods of low production. Improvements of the methodological strategy may be able to better quantify the contribution of food sources (autochthonous vs. allochthonous) to the biomass of chironomid larvae. Thus, the analysis of hydrogen stable isotope as a second isotopic tracer for chironomid remains

could better highlight the reliance on allochthonous OM (Doucett et al., 2007; Belle et al., 2015b).

Moreover, oxygen dynamics in lakes are closely related to climate change (Jankowski et al., 2006). Oxygen depletion in the profundal zone can be observed during warming events due to physical (i.e., stronger thermal stratification; Jankowski et al., 2006) and/or biological processes (i.e., higher bacterial degradation of sedimentary OM; den Heyer and Kalff, 1998). Under anoxic conditions, OM can be degraded to biogenic methane by methanogenic archaea (Borrel et al., 2011), and oxidized by methane-oxidizing bacteria. Methane-oxidizing bacteria then can be used as a food resource by chironomid larvae (Bunn and Boon 1993; Jones et al., 2008; Agasild et al., 2014). A significant incorporation of CH₄-derived carbon into chironomid biomass in Lake Tollari was found in connection with anoxic events during the Holocene Thermal Maximum (Belle et al., 2017b). Nevertheless, reconstruction of the carbon resources sustaining chironomid biomass in Lake Peipsi did not reveal significant contributions of CH₄-derived carbon to these benthic consumers (Fig. 2), even though that the target species (*C. plumosus*-type) was expected to feed on methane-oxidizing bacteria when available in the environment (Kelly et al., 2004). These results highlight the difference in the oxygen dynamics in the profundal zone of lakes with contrasting morphometry. Reconstruction of past oxygen dynamics in lakes from analysis of sub-fossil chironomid assemblages (Millet et al., 2010; Frossard et al., 2013b), and Fe/Mn ratio from XRF measurements (Schilder et al., 2017) could improve our understanding of the response of biogeochemical cycles to climate change.

4.3. Chironomid feeding behaviour vs. ecological process

Carbon stable isotopic composition of chironomid remains was analysed on two different morphotypes (*C. anthracinus*-type for Lake Tollari, and *C. plumosus*-type for Lake Peipsi), which are known to have complex feeding behaviours. Johnson (1985) classified *C. plumosus* larvae as filter feeders but it can easily switch from filter to deposit feeding (Hodkinson and Williams, 1980), whereas *C. anthracinus* larvae belong to the deposit feeder trophic guild. Johnson (1987) also demonstrated that the diet of *C. plumosus* larvae was more enriched in diatoms than *C. anthracinus* larvae during diatom blooms. This statement agreed with our results suggesting that chironomid biomass in Lake Peipsi was sustained only by aquatic pelagic primary production. Moreover, stable isotope studies conducted on *C. anthracinus* and *C. plumosus* also revealed strong seasonal and inter-individual variation in diet (Grey et al., 2004; Kelly et al., 2004), reflecting differences in their abilities to incorporate CH₄-derived carbon in their biomass. *C. plumosus* larvae seem more able to feed on methanotrophic production (Kelly et al., 2004) than *C. anthracinus*. In the present study, only chironomid biomass from Lake Tollari (belonging to the *C. anthracinus*-type morphotype) was supported by CH₄-derived carbon (Belle et al., 2017b), whereas no evidence of CH₄-derived carbon contribution to benthic consumer was found in the Lake Peipsi record (Fig. 2). Thus, differences in the temporal dynamics of changes in carbon resources fuelling chironomid biomass cannot be explained by different feeding strategies, and may be the consequences of food dynamics in the studied lakes.

5. Conclusions

Identification of carbon flows through food webs provides valuable insights on impacts of climate change on ecosystem functioning. Small lakes are known to be sensitive to past climate change, but very little is known about climate-induced changes in carbon resources that sustain benthic consumers in large lakes. We

reconstructed past dynamics of the phytoplankton community and carbon sources sustaining benthic consumers during the last 10,000 years by analysis of sedimentary pigments and carbon stable isotopic composition of chironomid remains in a large Lake Peipsi. Our results did not reveal any relationship with temperature fluctuations as previously found for small lakes, probably due to OM dynamics in the lake sediment. We hypothesize that long distance from the shoreline to the lake centre, and the large water volume make: first, allochthonous OM rare and refractory in the central zone of the lake; and second, aquatic primary producers more numerous for benthic consumers. Therefore, we suggest that lake morphometry can be an important environmental filter and mediate the effects of climatic change on benthic food webs of lakes, leading to lower sensitivity to climate change of carbon cycling in large lakes.

Acknowledgments

Financial support was provided by institutional research grants IUT1-8 and IUT21-2 from the Estonian Science Agency and by Estonian University of Life Sciences, project No. 8M160101PKLJ. We are grateful to Christian Hossann (INRA Nancy, Champenoux) for assistance in carbon stable isotope analysis. The PTEF facility is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-11-LABX-0002-01). We acknowledge the contributions of Atko Heinsalu, Siim Veski and Jüri Vassiljev for coring and sediment dating. We also thank G. L. Simpson for valuable comments on statistical analyses. Editing services were provided by Sea Pen Scientific Writing.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2018.03.027>.

References

- Agasild, H., Zingel, P., Tuvikene, L., Tuvikene, A., Timm, H., Feldmann, T., Salujõe, J., Toming, K., Jones, R.I., Nöges, T., 2014. Biogenic methane contributes to the food web of a large, shallow lake. *Freshw. Biol.* 59, 272–285.
- Anderson, N.J., Brodersen, K.P., Ryves, D.B., McGowan, S., Johansson, L.S., Jeppesen, E., Leng, M.J., 2008. Climate versus in-lake processes as controls on the development of community structure in a Low-Arctic lake (South-West Greenland). *Ecosystems* 11, 307–324.
- Anderson, N.J., D'Andrea, W., Fritz, S.C., 2009. Holocene carbon burial by lakes in SW Greenland. *Global Change Biol.* 15, 2590–2598.
- Belle, S., Luoto, T.P., Kivilä, H.E., Nevalainen, L., 2017a. Chironomid paleo diet as an indicator of past carbon cycle in boreal lakes: lake Kylmänpää (Kainuu province; Eastern Finland) as a case study. *Hydrobiol.* 785, 149–158.
- Belle, S., Millet, L., Gillet, F., Verneaux, V., Magny, M., 2015a. Assemblages and paleo-diet variability of subfossil chironomidae (Diptera) from a deep lake (Lake Grand Maclu, France). *Hydrobiol.* 755, 145–160.
- Belle, S., Tönno, I., Poska, A., Musazzi, S., Leys, B., Lami, A., 2018. Long-term effects of climate change on carbon flows through benthic secondary production in small lakes. *Freshw. Biol.* <https://doi.org/10.1111/fwb.13090> (in press).
- Belle, S., Poska, A., Hossann, C., Tönno, I., 2017b. 14,000 years of climate-induced changes in carbon resources sustaining benthic consumers in a small boreal lake (Lake Tollari, Estonia). *Climatic Change* 145, 209–215.
- Belle, S., Verneaux, V., Millet, L., Parent, C., Magny, M., 2015b. A case study of the past CH₄ cycle in lakes by the combined use of dual isotopes (carbon and hydrogen) and ancient DNA of methane-oxidizing bacteria: rearing experiment and application to Lake Remoray (Eastern France). *Aquat. Ecol.* 49, 279–291.
- Bennion, H., Simpson, G.L., Goldsmith, B.J., 2015. Assessing degradation and recovery pathways in lakes impacted by eutrophication using the sediment record. *Front. Ecol. Evol.* 3.
- Berggren, M., Bergström, A.-K., Karlsson, J., 2015. Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and fall. *PLoS One* 10 e0120575.
- Blenckner, T., 2005. A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia* 533, 1–14.
- Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The Identification and Use of Palaeoecological Chironomidae Larvae in Palaeoecology. Quaternary Research Association.
- Borrel, G., Jézéquel, D., Biderre-Petit, C., Morel-Desrosiers, N., Morel, J.-P., Peyret, P.,

- Fonty, G., Lehours, A.-C., 2011. Production and consumption of methane in freshwater lake ecosystems. *Res. Microbiol.* 162, 832–847.
- Bunn, S.E., Boon, P.L., 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* 96, 85–94.
- Carpenter, S.R., Cole, J.J., Pace, M.L., Van de Bogert, M., Bade, D.L., Bastviken, D., Gille, C.M., Hodgson, J.R., Kitchell, J.F., Kritzberg, E.S., 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology* 86, 2737–2750.
- Catalan, J., Pla, S., García, J., Camarero, L., 2009. Climate and CO_2 saturation in an Alpine Lake throughout the Holocene. *Limnol. Oceanogr.* 54, 2542–2552.
- Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert, M.C., Kitchell, J.L., Hodgson, J.R., 2006. Differential support of lake food webs by three types of terrestrial organic carbon. *Ecol. Lett.* 9, 558–568.
- Crenier, C., Arce-Funck, J., Bec, A., Billoir, E., Perrière, F., Leflaive, J., Guérol, F., Felten, V., Danger, M., 2017. Minor food sources can play a major role in secondary production in detritus-based ecosystems. *Freshw. Biol.* 62, 1155–1167.
- Deshpande, B.N., Tremblay, R., Pienitz, R., Vincent, W.F., 2014. Sedimentary pigments as indicators of cyanobacterial dynamics in a hypereutrophic lake. *J. Paleolimnol.* 52, 171–184.
- Digerfeldt, G., Håkansson, H., 1993. The Holocene paleolimnology of Lake Sjämsjön, southwestern Sweden. *J. Paleolimnol.* 8, 189–210.
- Doucett, R.R., Marks, J.C., Blinn, D.W., Caron, M., Hungate, B.A., 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. *Ecology* 88, 1587–1592.
- Frossard, V., Belle, S., Verneaux, V., Millet, L., Magny, M., 2013a. A study of the $\delta^{13}\text{C}$ offset between chironomid larvae and their exuvial head capsules: implications for palaeoecology. *J. Paleolimnol.* 50, 379–386.
- Frossard, V., Millet, L., Verneaux, V., Jenny, J.-P., Arnaud, F., Magny, M., Poulenard, J., Perga, M.-E., 2013b. Chironomid assemblages in cores from multiple water depths reflect oxygen-driven changes in a deep French lake over the last 150 years. *J. Paleolimnol.* 50, 257–273.
- Goedkoop, W., Akerblom, N., Demandt, M.H., 2006. Trophic fractionation of carbon and nitrogen stable isotopes in Chironomus riparius reared on food of aquatic and terrestrial origin. *Freshw. Biol.* 51, 878–886.
- Goedkoop, W., Johnson, R.K., 1992. Modelling the importance of sediment bacterial carbon for profundal macroinvertebrates along a lake nutrient gradient. *Neth J. Aqua Eco* 26, 477–483.
- Goedkoop, W., Johnson, R.K., 1996. Pelagic-benthic coupling: profundal benthic community response to spring diatom deposition in Mesotrophic Lake Erken. *Limnol. Oceanogr.* 41, 636–647.
- Goldman, C.R., Kumagai, M., Robarts, R.D., 2012. Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for Ecosystems and Societies. John Wiley & Sons.
- Grey, J., Kelly, A., Ward, S., Sommerwerk, N., Jones, R.I., 2004. Seasonal changes in the stable isotope values of lake-dwelling chironomid larvae in relation to feeding and life cycle variability. *Freshw. Biol.* 49, 681–689.
- Guilizzoni, P., Marchetto, A., Lami, A., Gerli, S., Musazzi, S., 2011. Use of sedimentary pigments to infer past phosphorus concentration in lakes. *J. Paleolimnol.* 45, 433–445.
- Guo, F., Kainz, M.J., Sheldon, F., Bunn, S.E., 2016. The importance of high-quality algal food sources in stream food webs – current status and future perspectives. *Freshw. Biol.* 61, 815–831.
- Hang, T., Kalm, V., Kihno, K., Milkevičius, M., 2008. Pollen, diatom and plant macrofossil assemblages indicate a low water level phase of Lake Peipsi at the beginning of the Holocene. *Hydrobiologia* 599, 13–21.
- Hang, T., Mädelc, A., Kalm, V., Kimmelbe, K., 2001. New data on the distribution and stratigraphy of the bottom deposits of Lake Peipsi, Eastern Estonia. *Proc. Est. Acad. Sci. Geol.* 50 (4), 233–253. Estonian Academy Publishers.
- van Hardenbroek, M., Heiri, O., Grey, J., Bodelier, P.L.E., Verbruggen, F., Lotter, A.F., 2009. Fossil chironomid $\delta^{13}\text{C}$ as a proxy for past methanogenic contribution to benthic food webs in lakes? *J. Paleolimnol.* 43, 235–245.
- van Hardenbroek, M., Heiri, O., Parmentier, F.J.W., Bastviken, D., Ilyashuk, B.P., Wiklund, J.A., Hall, R.I., Lotter, A.F., 2013. Evidence for past variations in methane availability in a Siberian thermokarst lake based on $\delta^{13}\text{C}$ of chitinous invertebrate remains. *Quat. Sci. Rev.* 66, 74–84.
- Hardenbroek, M. van, Lotter, A.F., Bastviken, D., Andersen, T.J., Heiri, O., 2014. Taxon-specific $\delta^{13}\text{C}$ analysis of chitinous invertebrate remains in sediments from Strandsjön, Sweden. *J. Paleolimnol.* 52, 95–105.
- den Heyer, C., Kalff, J., 1998. Organic matter mineralization rates in sediments: a within-and among-lake study. *Limnol. Oceanogr.* 43, 695–705.
- Hockun, K., Mollenhauer, G., Ho, S.L., Heffer, J., Ohlendorf, C., Zolitschka, B., Mayr, C., Lücke, A., Schefuß, E., 2016. Using distributions and stable isotopes of n-alkanes to disentangle organic matter contributions to sediments of Laguna Potrok Aike, Argentina. *Org. Geochem.* 102, 110–119.
- Hodkinson, I.D., Williams, K.A., 1980. Tube formation and distribution of Chironomus plumosus L. (Diptera: chironomidae) in a Eutrophic Woodland Pond. In: MURRAY, D.A. (Ed.), Chironomidae. Pergamon, pp. 331–337.
- Holmström, L., Ilvonen, L., Seppä, H., Veski, S., et al., 2015. A Bayesian spatiotemporal model for reconstructing climate from multiple pollen records. *Ann. Appl. Stat.* 9, 1194–1225.
- Huser, B.J., Fütter, M.N., Wang, R., Fölster, J., 2018. Persistent and widespread long-term phosphorus declines in Boreal Lakes in Sweden. *Sci. Tot. Env.* 613–614, 240–249.
- Ilvonen, L., Holmström, L., Seppä, H., Veski, S., 2016. A Bayesian multinomial regression model for palaeoclimate reconstruction with time uncertainty. *Environmetrics* 27, 409–422.
- Jankowski, T., Livingstone, D.M., Bührer, H., Forster, R., Niederhauser, P., 2006. Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: implications for a warmer world. *Limnol. Oceanogr.* 51, 815–819.
- Jansson, M., Persson, L., De Roos, A.M., Jones, R.I., Tranvik, L.J., 2007. Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends Ecol. Evol.* 22, 316–322.
- Johnson, R.K., 1985. Feeding efficiencies of Chironomus plumosus (L.) and C. Anthracinus zett. (Diptera: chironomidae) in Mesotrophic Lake Erken. *Freshw. Biol.* 15, 605–612.
- Johnson, R.K., 1987. Seasonal variation in diet of Chironomus plumosus (L.) and C. Anthracinus zett. (Diptera: chironomidae) in Mesotrophic Lake Erken. *Freshw. Biol.* 17, 525–532.
- Jones, R.I., Carter, C.E., Kelly, A., Ward, S., Kelly, D.J., Grey, J., 2008. Widespread contribution of methane-cycle bacteria to the diets of lake profundal chironomid larvae. *Ecology* 89, 857–864.
- Jones, R.I., Grey, J., Sleep, D., Quarmby, C., 1998. An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 265, 105–110.
- Kelly, A., Jones, R.I., Grey, J., 2004. Stable isotope analysis provides fresh insights into dietary separation between Chironomus anthracinus and C. plumosus. *J. N. Am. Benthol. Soc.* 23, 287–296.
- Kisand, A., Kirs, A.-L., Ehapalu, K., Alliksaar, T., Heinsalu, A., Tönno, I., Leeben, A., Nöges, P., 2017. Development of large shallow Lake Peipsi (North-Eastern Europe) over the Holocene based on the stratigraphy of phosphorus fractions. *J. Paleolimnol.* 58, 43–56.
- Lau, D.C.P., Sundh, I., Vrede, T., Pickova, J., Goedkoop, W., 2014. Autochthonous resources are the main driver of consumer production in dystrophic boreal lakes. *Ecology* 95, 1506–1519.
- Leavitt, P.R., Fritz, S.C., Anderson, N.J., Baker, P.A., Blenckner, T., Bunting, L., Catalan, J., Conley, D.J., Hobbs, W.O., Jeppesen, E., Korhola, A., McGowan, S., Rühland, K., Rusak, J.A., Simpson, G.L., Solovieva, N., Werne, J., 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. *Limnol. Oceanogr.* 54, 2330–2348.
- Leavitt, P.R., Hodgson, D.A., 2002. Sedimentary pigments. In: Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research. Springer, Dordrecht, pp. 295–325.
- Leeben, A., Heinsalu, A., Alliksaar, T., Vassiljev, J., 2010. High-resolution spectroscopic study of pore-water dissolved organic matter in Holocene sediments of Lake Peipsi (Estonia/Russia). *Hydrobiol.* 646, 21–31.
- Leeben, A., Tönno, I., Freiberg, R., Lepane, V., Bonningues, N., Makarõtševa, N., Heinsalu, A., Alliksaar, T., 2008. History of anthropogenically mediated eutrophication of Lake Peipsi as revealed by the stratigraphy of fossil pigments and molecular size fractions of pore-water dissolved organic matter. *Hydrobiol.* 599, 49–58.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 157–176.
- Magny, M., Leroux, A., Bichet, V., Gauthier, E., Richard, H., Walter-Simonnet, A.-V., 2012. Climate, vegetation and land use as drivers of Holocene sedimentation: a case study from Lake Saint-Point (Jura Mountains, Eastern France). *Holocene* 23, 137–147.
- Millet, L., Giguët-Covex, C., Verneaux, V., Druart, J.-C., Adatte, T., Arnaud, F., 2010. Reconstruction of the recent history of a large deep prealpine lake (Lake Bourget, France) using subfossil chironomids, diatoms, and organic matter analysis: towards the definition of a lake-specific reference state. *J. Paleolimnol.* 44, 963–978.
- Meyers, P.A., Ishiwatari, R., 1993. Lacustrine organic geochemistry—an overview of indicators of organic matter sources and diagenesis in lake sediments. *Org. Geochem.* 20, 867–900.
- Nogaro, G., Mermillod-Blondin, F., Valett, M.H., François-Carcaillet, F., Gaudet, J.-P., Lafont, M., Gibert, J., 2009. Ecosystem engineering at the sediment–water interface: bioturbation and consumer–substrate interaction. *Oecologia* 161, 125–138.
- Poska, A., Saarse, L., Veski, S., 2004. Reflections of pre- and early-agrarian human impact in the pollen diagrams of Estonia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 209, 37–50.
- Punning, J.-M., Koff, T., Kadastik, E., Mikomägi, A., 2005. Holocene lake level fluctuations recorded in the sediment composition of lake juusa, Southeastern Estonia. *J. Paleolimnol.* 34, 377–390.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>.
- Rantala, M.V., Luoto, T.P., Weckström, J., Perga, M.-E., Rautio, M., Nevalainen, L., 2015. Climate controls on the Holocene development of a Subarctic Lake in Northern Fennoscandia. *Quat. Sci. Rev.* 126, 175–185.
- Rautio, M., Mariash, H., Forsström, L., 2011. Seasonal shifts between autochthonous and allochthonous carbon contributions to zooplankton diets in a subarctic lake. *Limnol. Oceanogr.* 56, 1513–1524.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., et al., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 Years cal BP. *Radiocarbon* 55, 1869–1887.
- Reuss, N.S., Hammarlund, D., Rundgren, M., Segerström, U., Eriksson, L., Rosén, P., 2010. Lake Ecosystem Responses to Holocene Climate Change at the Subarctic Tree-Line in Northern Sweden. *Ecosystems* 13, 393–409.
- Salerno, F., Rogora, M., Balestrini, R., Lami, A., Tartari, G.A., Thakuri, S., et al., 2016.

- Glacier melting increases the solute concentrations of Himalayan glacial lakes. *Env Sc Tech* 50, 9150–9160.
- Schimmelmann, A., DeNiro, M.J., 1986. Stable isotopic studies on chitin. III. The D/H and $^{18}\text{O}/^{16}\text{O}$ ratios in arthropod chitin. *Geochim Cosmochim Acta* 50, 1485–1496.
- Schilder, J., van, Hardenbroek M., Bodelier, P., Kirilova, E.P., Leuenberger, M., Lotter, A.F., et al., 2017. Trophic state changes can affect the importance of methane-derived carbon in aquatic food webs. *Proc. R. Soc. B* 284, 20170278.
- Seppä, H., Poska, A., 2004. Holocene annual mean temperature changes in Estonia and their relationship to solar insolation and atmospheric circulation patterns. *Quaternary Res* 61, 22–31.
- Simpson, G.L., Anderson, N.J., 2009. Deciphering the effect of climate change and separating the influence of confounding factors in sediment core records using additive models. *Limnol. Oceanogr.* 54, 2529–2541.
- Smyntek, P.M., Maberly, S.C., Grey, J., 2012. Dissolved carbon dioxide concentration controls baseline stable carbon isotope signatures of a lake food web. *Limnol. Oceanogr.* 57, 1292–1302.
- Stankiewicz, B.A., Briggs, D.E.G., Evershed, R.P., Flannery, M.B., Wuttke, M., 1997. Preservation of chitin in 25-million-year-old fossils. *Science* 276, 1541–1543.
- Syväranta, J., Hämäläinen, H., Jones, R.I., 2006. Within-lake variability in carbon and nitrogen stable isotope signatures. *Freshw. Biol.* 51, 1090–1102.
- Tamm, M., Freiberg, R., Tönno, I., et al., 2015. Pigment-based chemotaxonomy - a quick alternative to determine algal assemblages in large shallow eutrophic lake? *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0122526> e0122526.
- Tanentzap, A.J., Kielstra, B.W., Wilkinson, G.M., Berggren, M., Craig, N., del, Giorgio PA., Grey, J., Gunn, J.M., Jones, S.E., Karlsson, J., Solomon, C.T., Pace, M.L., 2017. Terrestrial support of lake food webs: synthesis reveals controls over cross-ecosystem resource use. *Science Advances* 3 e1601765.
- Vadeboncoeur, Y., Zanden, M.J.V., Lodge, D.M., 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *Bioscience* 52, 44–54.
- Verbruggen, F., Heiri, O., Reichert, G.-J., Leeuw, J.W.D., Nierop, K.G.J., Lotter, A.F., 2009. Effects of chemical pretreatments on $\delta^{18}\text{O}$ measurements, chemical composition, and morphology of chironomid head capsules. *J. Paleolimnol.* 43, 857–872.
- Vuorio, K., Meili, M., Sarvala, J., 2006. Taxon-specific variation in the stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of lake phytoplankton. *Freshw. Biol.* 51, 807–822.
- Walker, I.R., 2001. Midge: chironomidae and related Diptera. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research*. Springer Netherlands, pp. 43–66.
- Waters, M.N., Smoak, J.M., Saunders, C.J., 2013. Historic primary producer communities linked to water quality and hydrologic changes in the Northern Everglades. *J. Paleolimnol.* 49, 67–81.
- Whiticar, M.J., 1999. Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. *Chem. Geol.* 161, 291–314.
- Wilkinson, G.M., Carpenter, S.R., Cole, J.J., Pace, M.L., Yang, C., 2013. Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. *Freshw. Biol.* 58, 2037–2049.
- Wooller, M.J., Pohlman, J.W., Gaglioti, B.V., Langdon, P., Jones, M., Walter Anthony, K.M., Becker, K.W., Hinrichs, K.-U., Elvert, M., 2012. Reconstruction of past methane availability in an Arctic Alaska wetland indicates climate influenced methane release during the past ~12,000 years. *J. Paleolimnol.* 48, 27–42.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat Methodol* 73, 3–36.